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# **Midshelf Fronts in the South Atlantic Bight and Their Influence on Seabird Distribution and Seasonal Abundance**

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*Abstract* Relationships of seabird distribution and abundance to continental shelf fronts off the southeastern United States were studied during a 15-month period in 1983–1984. Surface thermal fronts occur in the middle shelf domain (20–40-m depths) on the continental shelf of the South Atlantic Bight (Cape Hatteras, North Carolina, to Cape Canaveral, Florida).

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Midshelf fronts propagate south of Cape Hatteras following coolings events and persist from October through March. The monthly mean abundance of seabirds in the midshelf domain was correlated with the frequency of occurrence and extent of these fronts. Seabird abundance within the midshelf domain peaked during fall and winter when fronts were also most numerous and extensive (attaining 1,800-km lengths). Seabirds aggregate within 10 km of the front, with greatest densities ( $>150/\text{km}^2$ ) on the shoreward side. Seabird guilds displayed different affinities for the fronts. Zooplanktivorous phalaropes (*Phalaropus*) had a clumped distribution, highly correlated with changes in water surface temperature at the front ( $r = .614$ ,  $p < .01$ ). Some peak aggregations of piscivorous birds, namely the northern gannet (*Sula bassanus*), were associated with fronts while other peaks occurred elsewhere. Scavenging species (*Larus*) were evenly distributed across the shelf and showed a weak negative relationship with the front ( $r = -.477$ ,  $p < .10$ ). Both nearshore and pelagic species forage at midshelf fronts. The elevated levels of biological activity and higher biomasses at fronts may allow seabirds to forage efficiently, resulting in these apparent shifts from typical habitats.

**KEY WORDS:** fronts, seabirds, guilds, continental shelf, South Atlantic Bight, southeastern United States.

## Introduction

Elevated levels of biological productivity have been frequently observed at oceanic fronts (Pingree et al., 1974; Fournier et al., 1979; Iversen et al., 1979; Pingree, 1979; Floodgate et al., 1981; Parsons et al., 1981; Jacobsen et al., 1983). Higher biomasses associated with these fronts may be due to the accumulation of plankton arising from convergent circulation (Houghton and Marra, 1983) or to enhanced vertical mixing and upwelling of nutrients into the euphotic zone. Complementary nutrients supplied by two adjacent water masses may also enhance productivity at fronts (Beardall et al., 1978).

Fronts have been defined as zones of contact between water masses of different densities, between mixed and stratified wa-

ters, or between water masses having thermoclines at different depths (Uda, 1959). Fronts may arise from several physical processes depending upon location. Inputs of freshwater (Bowman and Iversen, 1978), confluences (Pingree and Griffiths, 1978), and/or tidal/surface shear (Simpson and Pingree, 1978) influence their formation. Fronts are found from shallow to deep water over the continental shelf (Bowman and Esaias, 1978; Allen et al., 1983), and in pelagic waters (Cromwell and Reid, 1956; Knauss, 1957; Voorhis, 1969; Colton et al., 1975). Nearshore and continental shelf break fronts have been described for the continental shelf off the southeastern United States (Allen et al., 1983). We report here for the first time the annual variation of midshelf fronts on the continental shelf within this region.

Seabirds generally occupy tertiary positions in marine food webs, and it is reasonable to assume that they are affected by the biological interactions at fronts. Seabirds have been found to associate with fronts in boreal and temperate water masses (Ainley and Jacobs, 1981; Bourne, 1981; Schneider, 1982; Kinder et al., 1983). The interactions of seabirds with shallow sea fronts in a subtropical region are described here. Seabird-front associations were investigated by addressing four general questions:

1. What are the temporal and spatial patterns of midshelf fronts in the South Atlantic Bight?
2. Do seabirds show a spatial affinity for these fronts?
3. Do seabirds respond to the seasonal changes in the number and size of these fronts?
4. Do seabird species differ in their affinity for fronts?

## Materials and Methods

For the period February 1983 to April 1984, midshelf fronts off the southeastern United States were analyzed using National Oceanic and Atmospheric Administration (NOAA) Gulf Stream System Flow Charts ( $N = 151$ ) available three times a week. Surface thermal boundaries exceeding  $0.75^{\circ}\text{C}/\text{km}$  are contoured on 30-min latitude/longitude blocks using satellite infrared reflectance data. Using these charts we calculated the numbers and

lengths of fronts each month. Length was measured directly from the charts with a planimeter. Because satellite detection of fronts depends on the number of cloud-free days, the number of charts per month supplying frontal data varied. To permit comparisons between months and seasons, we standardized both number and length of fronts by expressing them as a function of the number of satellite map days (SMD) from which data were obtained.

Seabird surveys based on 15-min counting periods were made between 30° and 32° N latitude from February 1983 to April 1984 (Table 1). Each count represented one horizontal transect conducted while the vessel proceeded at 8–10 knots on a constant course and heading. Ship location and speed were recorded at the beginning and end of each transect. For cross-shelf sections, the transects were continuous and consecutive to enable close resolution of the dependence of seabird aggregations on physical oceanographic features.

For density estimates, all birds were counted out to a distance of 300 m from the observer and within the 90° bow sector on the side of the ship with the best viewing conditions (e.g., less glare). The surface area censused was calculated by multiplying the length of the transect (in kilometers) by 0.3 km. Width of the transect was determined with a hand-held rangefinder (Heinemann, 1981). Birds not in the transect zone were counted but not included in density estimates. Ship-following seabirds were excluded from counts. Bias arising from multi-observer counting was minimized by a single person (Haney) recording more than 95% of the 438 transects.

Depth measurements were made with a SIMRAD EL fathometer set to 2-m sensitivity scale. Water surface temperatures were recorded to the nearest 0.2°C with a bucket thermometer or Wheatstone bridge thermistor towed continuously at a depth of 0.5 m. Changes in water surface temperature were calculated using the formula  $\Delta T = |T_0 - T_1|$ , where  $T_0$  = water surface temperature at the start of the transect and  $T_1$  = water surface temperature at the end of the transect. Cross-shelf changes in seabird density were then plotted against changes in water surface temperature ( $\Delta T$ ) for each transect.

Differences in seasonal (quarterly) seabird density and in the

**Table 1**  
Seabird Sampling Effort in the Midshelf Domain of the South Atlantic  
Bight During 1983 and 1984

	No. Cruises	No. Transects	No. Census Days	km <sup>2</sup>	Vessels <sup>a</sup>	Cruise Objectives <sup>b</sup>
February	4	56	7	79.14	A,B	G,Z
March	2	44	4	36.47	A,B	G,Z
April	2	25	9	21.35	B,C	G,M,Z
May	2	54	8	58.92	A,C,D	G,M
June	1	21	5	25.98	B	G
July	1	53	5	49.77	A	M,Z
August	2	44	7	40.49	A,B	G,Z
September	4	60	5	78.10	A,C	M,Z
October	2	33	13	74.86	A,C	M,Z
November	2	19	3	24.71	A	Z
December	2	29	4	37.81	A,B	G

<sup>a</sup> A = 21-m R/V *Bluefin* (Skidaway Institute of Oceanography); B = 23-m R/V *Bulldog* (University of Georgia); C = 41-m R/V *Cape Hatteras* (Duke Oceanographic Consortium); D = 48-m R/V *Delaware II* National Marine Fisheries Service (NOAA/NMFS).

<sup>b</sup> G = groundfish survey, M = microbial research, Z = zooplankton research.

frequency and extent of fronts were assessed by one-way analysis of variance (ANOVA) for samples of unequal sizes (Snedecor and Cochran, 1980). Relationships of seabird abundance (density) to changes in water surface temperature were measured with simple correlation ( $r$ ). Correlation analyses were also used to compare monthly seabird densities to monthly frontal occurrence and extent. No transformations of data were applied for correlative tests. The nonparametric Mann-Whitney  $U$  test was used to test for significant differences between seabird density in nearfront (within 10 km) and remaining transects. Changes in habitat selection of *Sula bassanus* and *Puffinus lherminieri* were analyzed with Student's  $t$  tests for samples with unequal variances. Statistical analyses were done with a StatPak II program on a Hewlett-Packard 9825A computer. Statistical significance was set at  $p < .05$ . Green's (1966) coefficient of dispersion was

used to measure the degree of cross-shelf spatial clumping in three seabird guilds. This coefficient is computed using the formula  $[(s^2/\bar{x}) - 1]/\Sigma x - 1$ , where  $s^2$ ,  $\bar{x}$ , and  $\Sigma x$  are, respectively, the sample variance, mean, and total sample number.

## Results

### *Physical Dynamics of Midshelf Fronts*

Midshelf fronts exhibited variation ranging over daily to monthly to interannual time scales. The seasonal (quarterly) variation in the number and length of midshelf fronts during the 1983–1984 study period is shown in Table 2. Statistically significant seasonal variations in front frequency (one-way ANOVA,  $F = 10.514$ ,  $p < .001$ ) and front length (one-way ANOVA,  $F = 4.984$ ,  $p < .05$ ) were detected. Figure 1 illustrates the progression and persistence of fronts at roughly 2-week intervals throughout the fall, winter, and spring when cloud conditions permitted their observation. Seasonal frontogenesis typically begins south of Cape Hatteras off the Carolinas during September and October. Midshelf fronts attain their greatest spatial extent (in excess of 1,800-km lengths) during late fall and midwinter (November–February). Regionwide frontolysis occurs in spring (March–May) as frontal frequency and spatial extent decrease.

In late winter midshelf fronts become more convoluted and move across the shelf over weekly time spans (Figure 2). Both the midshelf and Gulf Stream western boundary front exhibit similar configurations during such periods.

The within-season persistence of fronts (measured by the percentage of SMDs with midshelf fronts) varied interannually, although not in the two February–April time periods in which seabird counts were conducted (39% in 1983 vs. 38% in 1984). During the fall frontogenesis period (October–December), however, fronts occurred in 51% of the SMDs in 1983 compared to 35% in 1984.

Shipboard measurements during cross-shelf sections (Figure 3) indicate that midshelf fronts are regions of strong horizontal

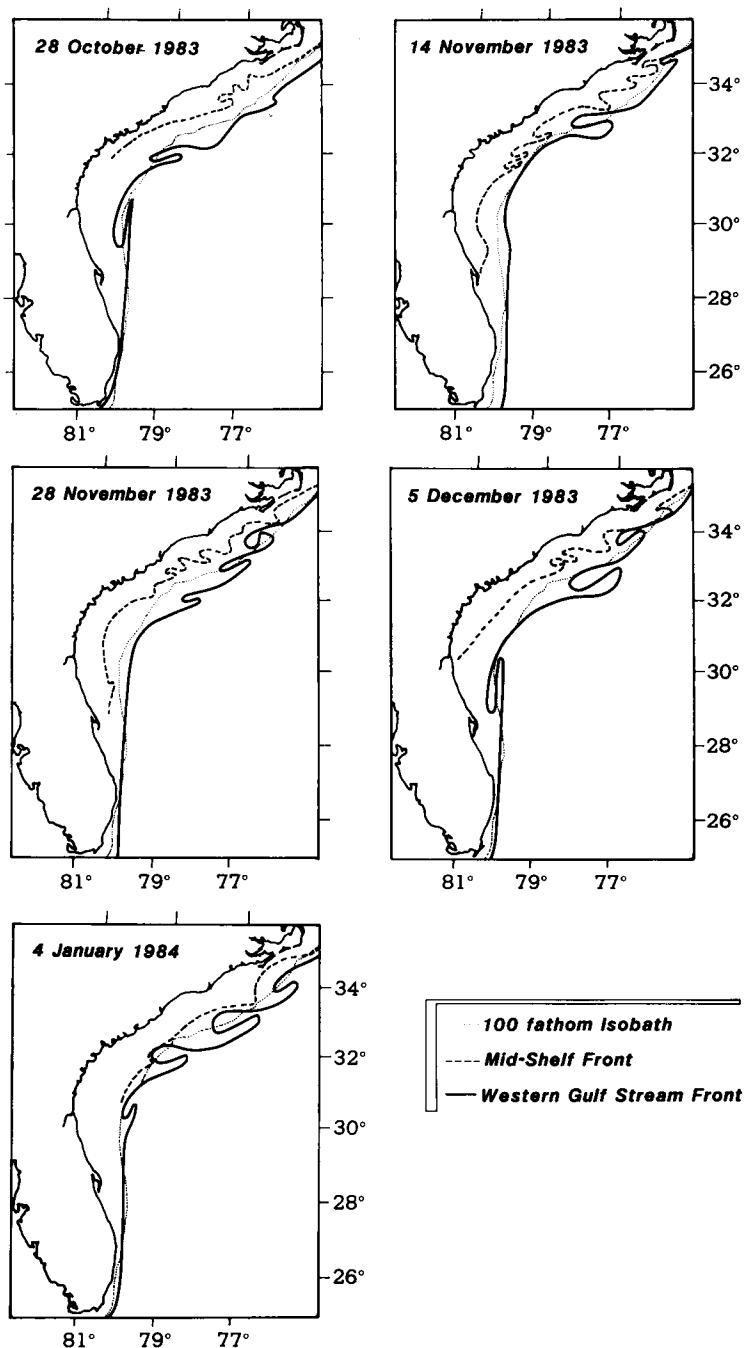
**Table 2**  
Seasonal Differences in the Number and Length (km) of  
Midshelf Fronts in the South Atlantic Bight

	No. Fronts/SMD		Front Length/SMD	
	$\bar{x}$	Range	$\bar{x}$	Range
Dec.–Feb.	0.49	0.33–0.57	487	383–552
Mar.–May	0.27	0.08–0.38	152	61–190
June–Aug.	0.03	0.00–0.08	8	0–25
Sept.–Nov.	0.70	0.42–0.84	423	123–635

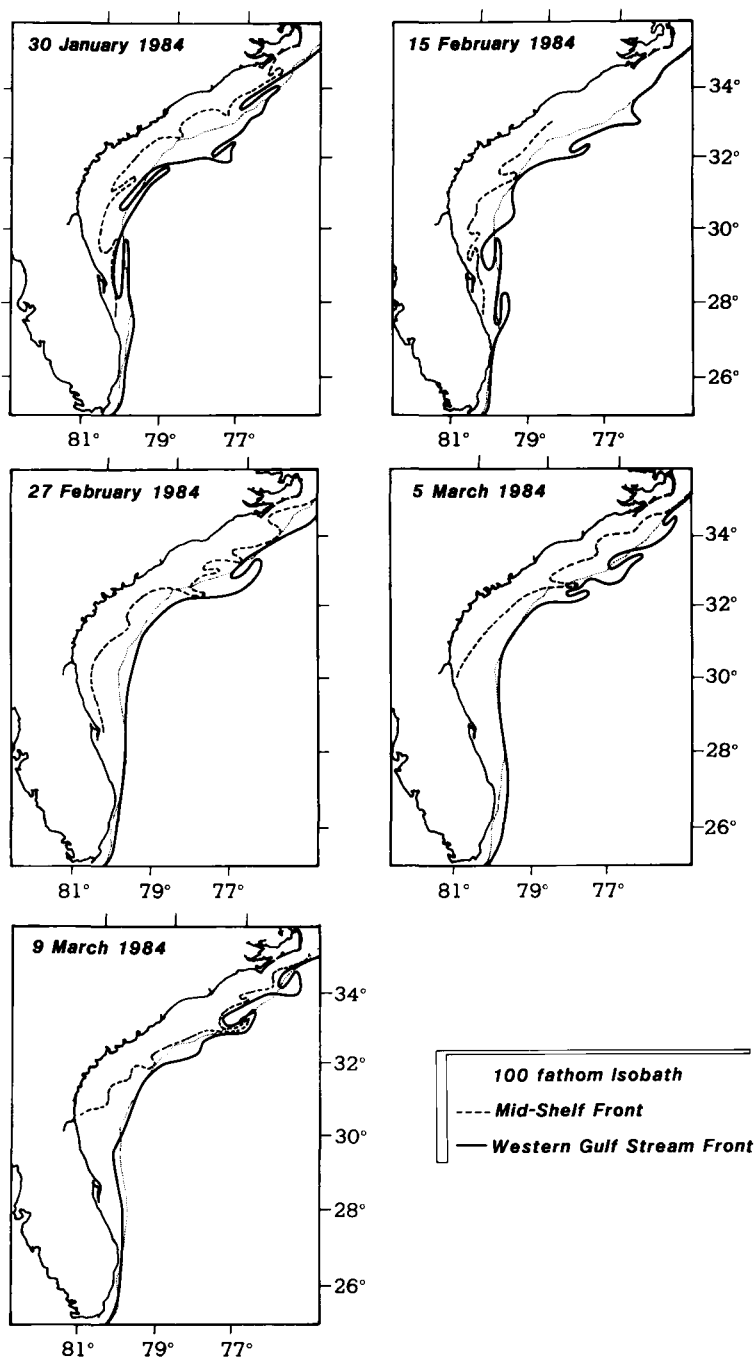
surface temperature gradients (Figure 4). On 1 February 1984 the surface temperature increased from 9.0° to 14.0°C over 20 km (1.0°C/5 km). Nearshore and outer shelf waters were characterized by much lower gradients of 0.1–0.2°C/5 km. On 21 November 1983, the surface temperature gradients at the front were 1.1°C/5 km compared to 0.2°C/5 km in nearshore and outer shelf waters.

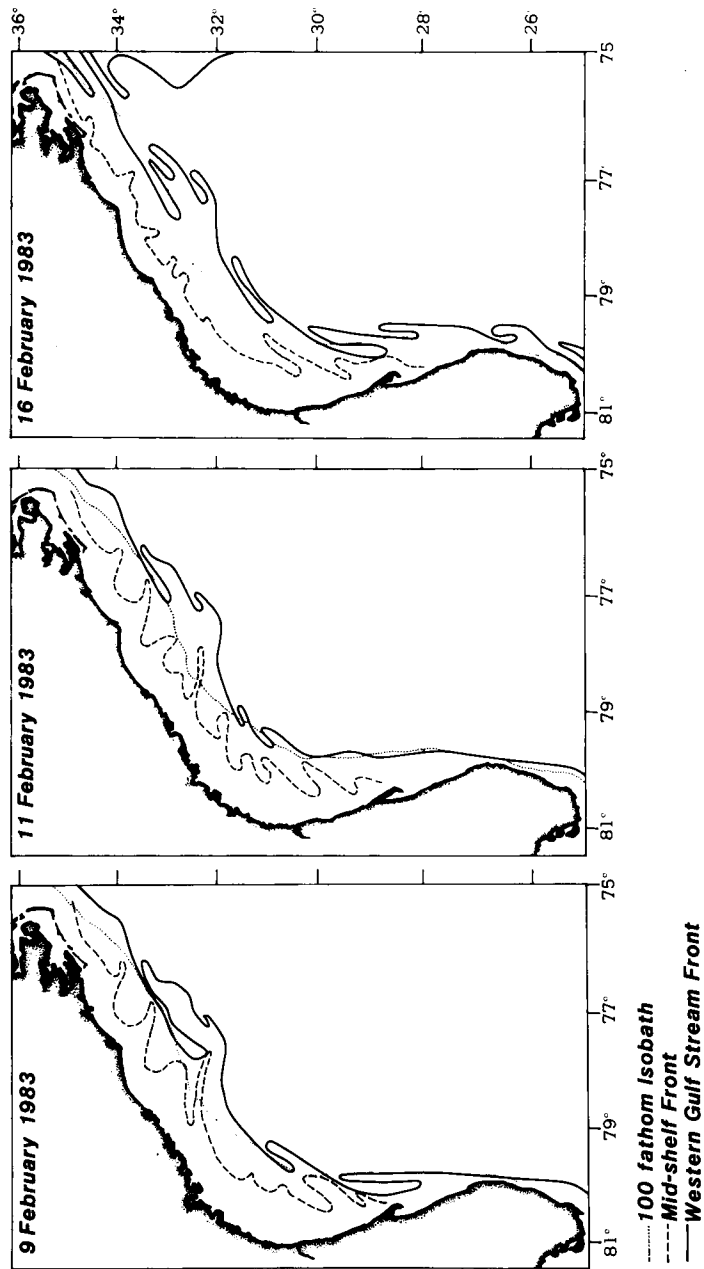
### *Seabird Distribution and Midshelf Fronts*

Seabirds were found to aggregate at the midshelf front on both the 21 November and 1 February cross-shelf sections (Figure 4). One of two peaks in bird density on 21 November and two of three peaks on 1 February corresponded to locations with strong surface water temperature gradients (thermal fronts). Significant correlations between seabird density and changes in water surface temperature were obtained on the entire 1 February cross-shelf section ( $r = .582$ ,  $p < .01$ ,  $df = 19$ ), but not on the entire 21 November section ( $r = .185$ ,  $p < .50$ ,  $df = 19$ ). When inshore transects (0–20-m depth) were excluded from correlation analysis, significant correlations were obtained for both sections ( $r = .753$ ,  $p < .001$ ,  $df = 16$  for 21 November;  $r = .577$ ,  $p < .05$ ,  $df = 11$  for 1 February). Inshore density peaks on 21 November (Transects 1–5; left side of Figure 4) were a result of seabirds, mostly scavenging *Larus*, associated with fishing vessels. The peak in

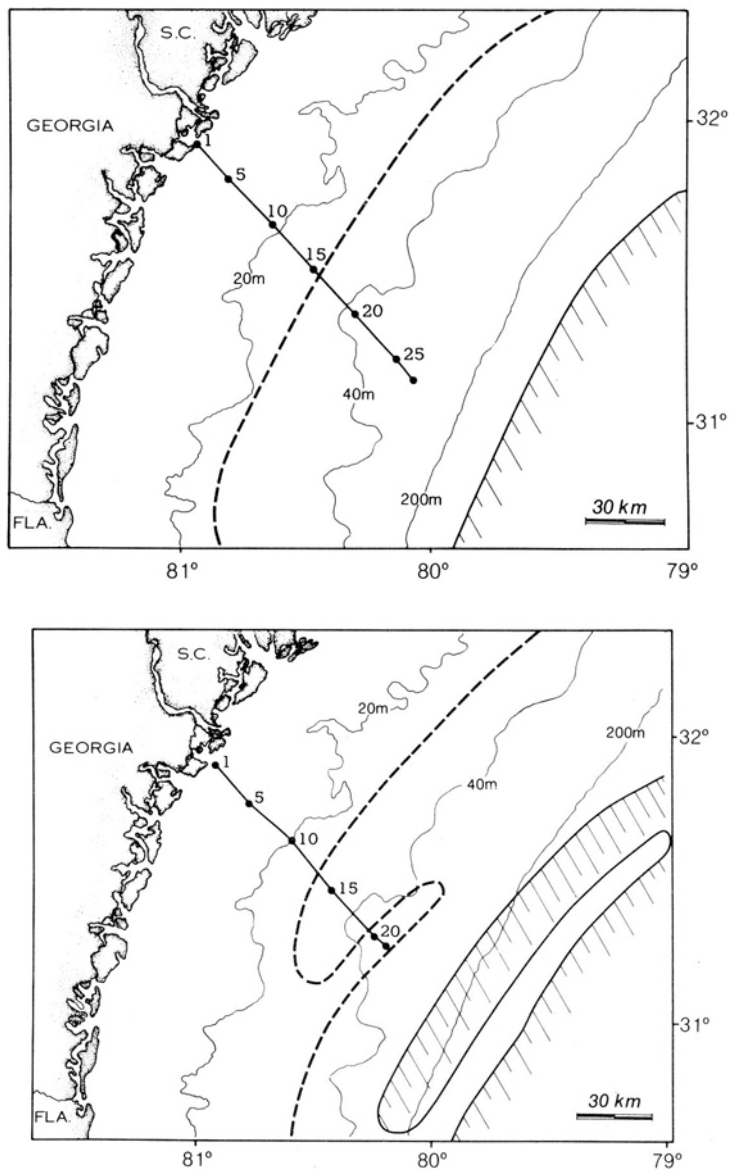


**FIGURE 1.** Seasonal persistence of midshelf fronts (*dashed lines*). Fronts are shown relative to the shelf and western Gulf Stream front (*solid line*).

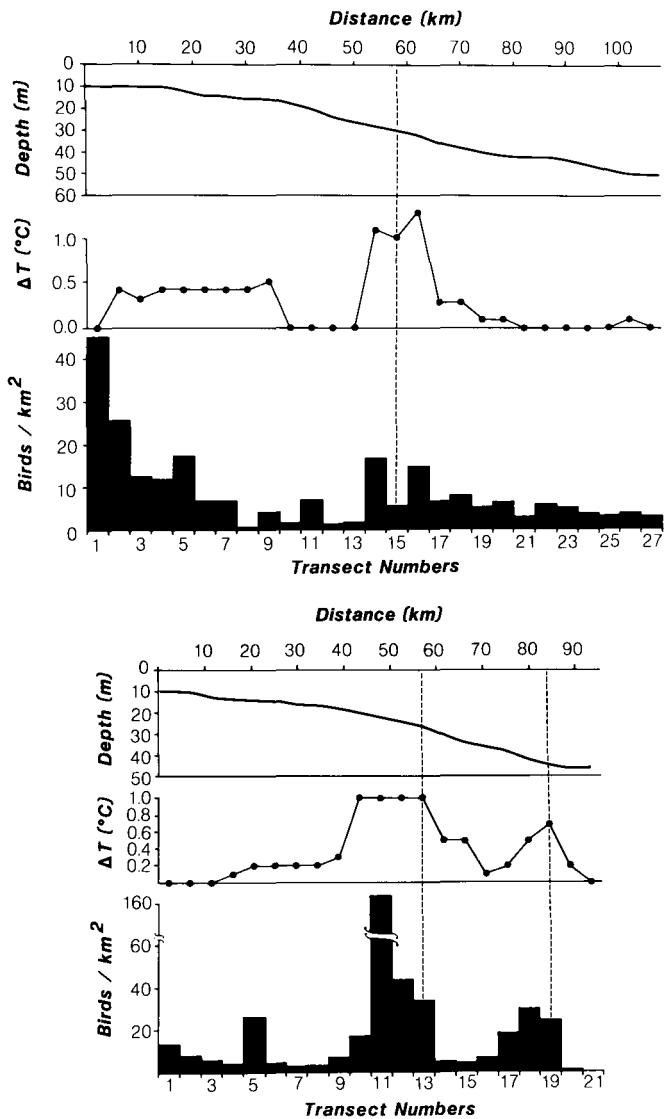




**FIGURE 2.** Time series of a midshelf front in winter showing frontal dynamics. Onshore movement is apparent during the 7-day period.



**FIGURE 3.** Cruise track of cross-shelf section in the southern South Atlantic Bight on (*top*) 21 November 1983 and (*bottom*) 1 February 1984. The location of the midshelf front (*dashed line*) and western Gulf Stream front (*solid line*) are derived from satellite data.



**FIGURE 4.** (top) Density of all seabirds during the 108-km cross-shelf section on 21 November 1983. The satellite-derived location of the midshelf front is shown at Transect 15. Transect numbers correspond to those in the top part of Figure 3. (bottom) Density of all seabirds during the 90-km cross-shelf section on 1 February 1984. The satellite-derived location of the midshelf front is shown at Transects 13 and 19. Transect numbers correspond to those in the bottom part of Figure 3.

inshore density on 1 February (Transect 5; right side of Figure 4) represented a single flock of *Sula bassanus* feeding on shoaling bait fish.

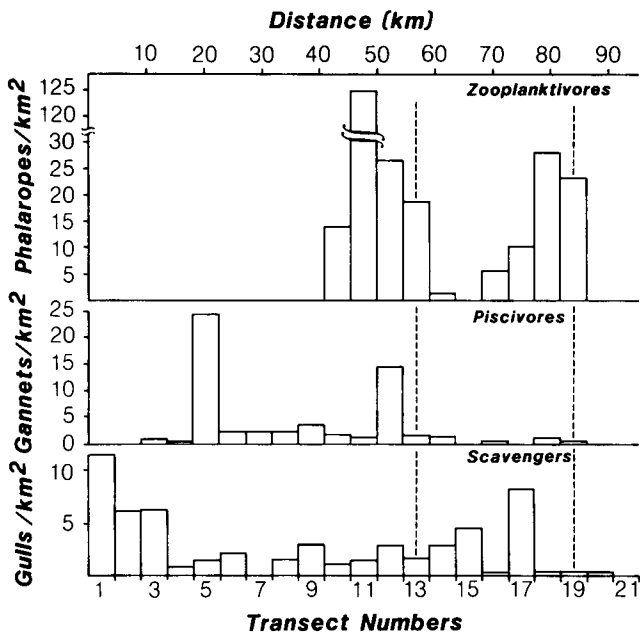
Aggregations of seabirds on 1 February were found mainly on the shoreward side of the front (right side of Figure 4). A peak of 160 birds/km<sup>2</sup> occurred at Transect 11. To compare the density of seabirds in frontal and nonfrontal regions we used the non-parametric Mann-Whitney *U* test, which allows comparisons of medians from two small-sample populations. We compared densities in transects within 10 km shoreward of the front to the remaining midshelf transects. Average density of seabirds in these nearfront transects was significantly higher (52 vs. 7:  $p < .005$ ,  $N = 6, 15$ ,  $z = 3.04$ ) than in other transects.

Seabirds associate with fronts in alongshore (length) as well as cross-shelf (width) dimensions. The two peaks in density at Transects 13 and 19 (right side of Figure 4) on 1 February occurred at the same front. Satellite data revealed, however, that this front was convoluted, turning to the northeast before again turning back to the southwest (bottom part of Figure 3), and aggregations of seabirds were found at both frontal crossings.

Seabird species that typically occur in nearshore and more pelagic habitats forage in the midshelf domain during periods of frontal activity. We compared differences in habitat selection of two species when midshelf fronts were frequent (October–February) and when they were infrequent (March–September). Depth at the location where individuals were observed was convenient for characterizing the cross-shelf habitat preferences of *Puffinus lherminieri* and *Sula bassanus* (Table 3). Other species either occurred during restricted time frames or in insufficient numbers for statistical treatment. *Puffinus lherminieri* is characteristic of tropical pelagic waters off the southeastern United States, that is, the Gulf Stream and outer shelf (Clapp et al., 1982; Haney, unpublished data). When fronts were present in the midshelf domain, this species was found much further inshore in shallower water (Table 3). *Sula bassanus* exhibited an opposite but equally significant shift. This species is found principally in nearshore waters (Clapp et al., 1982; Lee and Haney, 1984) but occurred further offshore in the midshelf domain when fronts were present (Table 3; Figure 5).

**Table 3**  
Cross-Shelf Distribution (measured as a function of mean depth,  $\bar{x}$ , in meters) of Two Seabird Species in Response to Frontal Occurrence

	Frontal Occurrence						<i>t</i>	<i>p</i>	<i>df</i>
	Frequent			Infrequent					
	$\bar{x}$	SD	<i>N</i>	$\bar{x}$	SD	<i>N</i>			
<i>Puffinus lherminieri</i>	41	6	120	207	171	215	10.57	<.001	333
<i>Sula bassanus</i>	22	4	532	11	3	162	32.87	<.001	692



**FIGURE 5.** Variation in dispersion of three seabird guilds around a midshelf front located at Transects 13 and 19 on 1 February 1984. Cross-shelf temperature gradients are identical with those on the right side of Figure 4.

*Seasonal Seabird Abundance and Fronts*

Seabird abundance in the midshelf domain varied markedly between seasons and months. One-way ANOVA revealed only weak ( $F = 2.311$ ,  $p < .15$ ) variation in quarterly seabird abun-

dance, due primarily to a proportionately higher contribution of the within-season component of variance. Numbers of seabird species and individuals in the midshelf domain were higher in winter and fall (Table 4) when fronts were also most frequent and extensive (see Table 2). Mean seabird density in spring and summer was less than one bird/km<sup>2</sup>, an order of magnitude lower than fall and winter values.

Monthly variation in seabird abundance and front frequency and extent are shown in Figure 6. To test linear relationships of seabird abundance with front frequency and extent, we used simple correlation ( $r$ ). Results of these tests indicated that monthly seabird density in the midshelf domain was significantly correlated with monthly front length ( $r = .611, p < .05, df = 9$ ). Monthly seabird density and monthly front frequency were not significantly correlated at the 5% level ( $r = .523, p < .10, df = 9$ ). The probability was almost significant and the small sample size reduces the power of this test, thereby increasing the risk of Type II error (erroneous acceptance of the null hypothesis).

If monthly seabird abundance varied similarly in adjacent portions of the shelf not influenced by the fronts, spurious correlations might be indicated. Seasonal changes in midshelf seabird abundance could, for example, be due to some extrinsic factor alone (e.g., a regionwide influx of seabirds from annual migration), independent of local conditions. To check for this type of error, monthly seabird abundance data from the outer shelf (40–200-m depths) were examined. Monthly seabird densities in this region of the shelf ranged from 1.32 to 4.81 birds/km<sup>2</sup>. Compared to this outer shelf domain, significantly higher variation (one-tailed test,  $F = 20.647, p < .005$ ) occurred in the midshelf region where fronts exhibited seasonality.

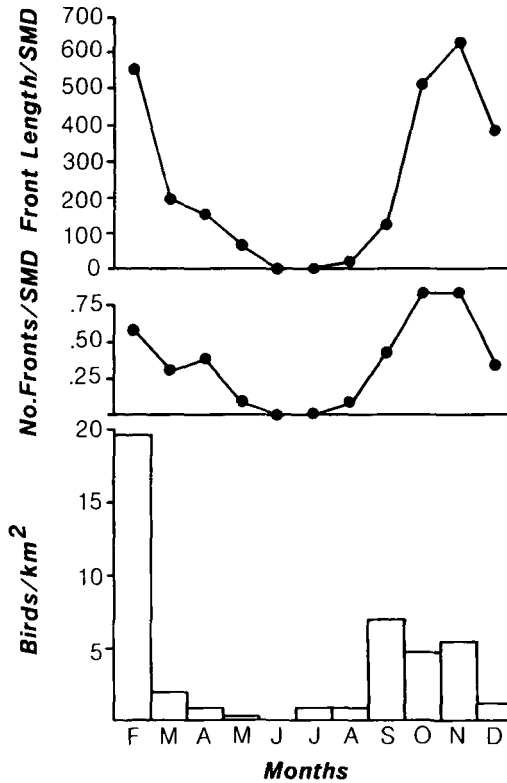
### *Seabird Guild Affinities for Fronts*

Seabird species feed on a variety of marine organisms and may be functionally grouped into guilds based on their major prey. We classified species recorded on the 1 February cross-shelf section into three guilds based on previous reviews (Ashmole, 1971; Ainley, 1977; Clapp et al., 1982). The species composition, density, and percent occurrence of a zooplanktivorous, piscivorous,

**Table 4**  
Seasonal Variation in Species Composition, Total Number (*N*), and Density ( $\text{km}^{-2}$ ) of  
Seabirds in the Midshelf Domain

	Dec.–Feb.		Mar.–May		June–Aug.		Sept.–Nov.	
	<i>N</i>	Density	<i>N</i>	Density	<i>N</i>	Density	<i>N</i>	Density
<i>Gavia stellata</i>	0	0.00	1	0.01	0	0.00	0	0.00
<i>G. immer</i>	41	0.35	5	0.04	0	0.00	13	0.07
<i>Fulmarus glacialis</i>	5	0.04	0	0.00	0	0.00	0	0.00
<i>Calonectris diomedea</i>	0	0.00	0	0.00	22	0.17	258	1.45
<i>Puffinus puffinus</i>	2	0.02	0	0.00	0	0.00	2	0.01
<i>P. lherminieri</i>	16	0.14	2	0.02	9	0.07	82	0.46
<i>Oceanites oceanicus</i>	0	0.00	2	0.02	2	0.02	0	0.00
<i>Phaethon lepturus</i>	0	0.00	0	0.00	0	0.00	1	0.01
<i>Sula dactylatra</i>	0	0.00	0	0.00	1	0.01	1	0.01
<i>S. bassanus</i>	72	0.66	0	0.00	0	0.00	0	0.00
<i>Phalaropus lobatus</i>	260	2.22	0	0.00	0	0.00	39	0.22
<i>P. fulicaria</i>	690	5.90	0	0.00	0	0.00	3	0.02
<i>Phalaropus</i> sp.	383	3.27	0	0.00	1	0.01	0	0.00
<i>Stercorarius pomarinus</i>	2	0.02	0	0.00	0	0.00	5	0.03

<i>S. parasiticus</i>	0	0.00	2	0.02	0	0.00	2	0.01
<i>Stercorarius</i> sp.	0	0.00	0	0.00	0	0.00	1	0.01
<i>Larus atricilla</i>	0	0.00	29	0.25	2	0.02	48	0.27
<i>L. philadelphia</i>	67	0.57	8	0.07	0	0.00	0	0.00
<i>L. argentatus</i>	37	0.32	26	0.22	0	0.00	19	0.11
<i>L. hyperboreus</i>	1	0.01	0	0.00	0	0.00	0	0.00
<i>Rissa tridactyla</i>	13	0.11	0	0.00	0	0.00	0	0.00
gull sp.	5	0.04	0	0.00	0	0.00	0	0.00
<i>Sterna maxima</i>	0	0.00	2	0.02	3	0.02	2	0.01
<i>S. sandvicensis</i>	0	0.00	0	0.00	1	0.01	2	0.01
<i>S. hirundo</i>	0	0.00	4	0.03	7	0.06	387	2.18
<i>S. forsteri</i>	0	0.00	0	0.00	0	0.00	1	0.01
<i>S. antillarum</i>	0	0.00	0	0.00	1	0.01	0	0.00
<i>S. anaethetus</i>	1	0.01	3	0.03	24	0.19	37	0.21
<i>Chlidonias niger</i>	0	0.00	1	0.01	3	0.02	115	0.65
<i>Anous stolidus</i>	0	0.00	0	0.00	0	0.00	1	0.01
<i>Alca torda</i>	2	0.02	0	0.00	0	0.00	0	0.00
Total	1,597	13.66	85	0.87	76	0.59	1,019	5.73



**FIGURE 6.** Relationship of monthly mean midshelf seabird density to monthly number and length of midshelf fronts per satellite map day (SMD) in the South Atlantic Bight.

and scavenging guild are summarized in Table 5. The three guilds showed varying degrees of cross-shelf clumping and affinity for the midshelf front (see Figure 5).

We measured the degree of clumping (or dispersion) with the coefficient developed by Green (1966), the only index of dispersion not dependent on sample mean, sample size, and total sample numbers (Elliott, 1977). Values for this index range from 0 for random dispersion to 1 for maximum contagion or clumping. Values obtained for the scavenging guild (0.043), piscivorous guild (0.202), and zooplanktivorous guild (0.246) indicated differential cross-shelf dispersion for these groups.

When we regressed densities of the three guilds to cross-shelf changes in water surface temperature ( $\Delta T$ ), only zooplanktivores were significantly correlated ( $r = .614$ ,  $p < .005$ ,  $df = 19$ ). Piscivores ( $r = .187$ ,  $p < .50$ ,  $df = 19$ ) and scavengers ( $r = -.268$ ,  $p < .50$ ,  $df = 19$ ) were not correlated with cross-shelf  $\Delta T$ s. When only midshelf transects were analyzed, however, the probability of Type I error decreased for correlations of both piscivores ( $r = .422$ ,  $p < .20$ ,  $df = 11$ ) and scavengers ( $r = -.477$ ,  $p < .10$ ,  $df = 11$ ).

## Discussion

### Seabird Attraction to Midshelf Fronts

Although seabird-front associations have been demonstrated repeatedly (Ainley and Jacobs, 1981; Schneider, 1982; Kinder et al., 1983; Haney and McGillivray, 1985), the mechanisms responsible

**Table 5**  
Species Composition, Density ( $\text{km}^{-2}$ ), and Percent Occurrence of  
Three Seabird Guilds in Nearfront ( $<10$  km) and Other Transects  
During the February 1984 Cross-Shelf Section

	Nearfront Transects			Other Transects		
	<i>N</i>	Density	%*	<i>N</i>	Density	%*
<b>Zooplanktivores</b>						
<i>Phalaropus lobatus</i>	240	16	60	0	0	0
<i>P. fulicaria</i>	278	19	50	0	0	0
<i>Phalaropus</i> sp.	162	11	60	40	3	9
Total	680	46	70	40	3	9
<b>Piscivores</b>						
<i>Sula bassanus</i>	57	4	70	57	4	72
<b>Scavengers</b>						
<i>Larus atricilla</i>	0	0	0	1	0.1	9
<i>L. philadelphia</i>	39	3	70	38	2	54
<i>L. argentatus</i>	7	0.5	50	21	1	82
<i>Rissa tridactyla</i>	4	0.3	30	0	0	0
Total	50	4	90	60	3	91

\*Percent of transects in which the taxon was observed.

for these associations are imperfectly known. We postulate that seabird prey items at midshelf fronts originate from environmental conditions caused by subsurface Gulf Stream intrusions and are subsequently made available to surface-foraging seabirds owing to secondary physical processes involving vertical transport.

Phytoplankton standing crops within the midshelf zone result from subsurface or bottom intrusions of cooler, deep nutrient-rich Gulf Stream waters (Blanton et al., 1981; Yoder et al., 1981; Yoder et al., 1983), and high zooplankton stocks occur in response to this phytoplankton growth (Paffenhofer, 1980; Paffenhofer et al., 1984). Unlike the continental shelf north of Cape Hatteras where phytoplankton blooms are seasonal (Sverdrup, 1953; Ryther and Yentsch, 1958; Riley, 1959; Smayda, 1973), plankton-rich intrusions occur episodically in the South Atlantic Bight throughout the period May through October (Paffenhofer et al., 1984; Yoder, 1985).

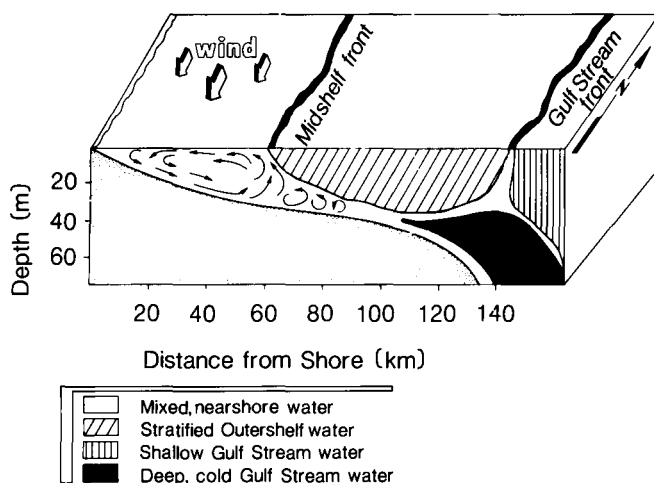
Zooplankton, such as *Temora* spp., *Eucalanus pileatus*, *Centropages furcatus*, *Candacia armata*, *Conchoecia*, and *Sagitta enflata* (Bowman, 1971), are primarily restricted to bottom waters at or below the thermocline because of seasonal stratification (Bumpus, 1955; Blanton, 1971; Stefansson et al., 1971; Atkinson et al., 1980). Well-mixed nearshore waters on the shoreward side of the midshelf front would result in circulation patterns conducive to vertical transport of zooplankton from the thermocline to or near the surface (Bowman, 1978; Garvine, 1980), particularly during periods of northerly alongshore winds (Figure 7). Doming isotherms on the shoreward side of a typical midshelf front (Figure 8) demonstrate that divergence may occur.

Higher biomasses of some zooplankton, especially larval Clupeiform fish (J. A. Yoder, unpublished data) and the copepod *Eucalanus pileatus* (G.-A. Paffenhofer, unpublished data), occur on the shoreward side of the front. Seabird species with the highest affinity for the front were zooplanktivorous phalaropes (Dodson and Egger, 1980) that are restricted to the ocean surface during feeding (Ainley and Sanger, 1979; Ridley, 1980). Phalaropes have been previously related to oceanic fronts or similar regions of divergence (Brown, 1977, 1980a; Briggs et al., 1984).

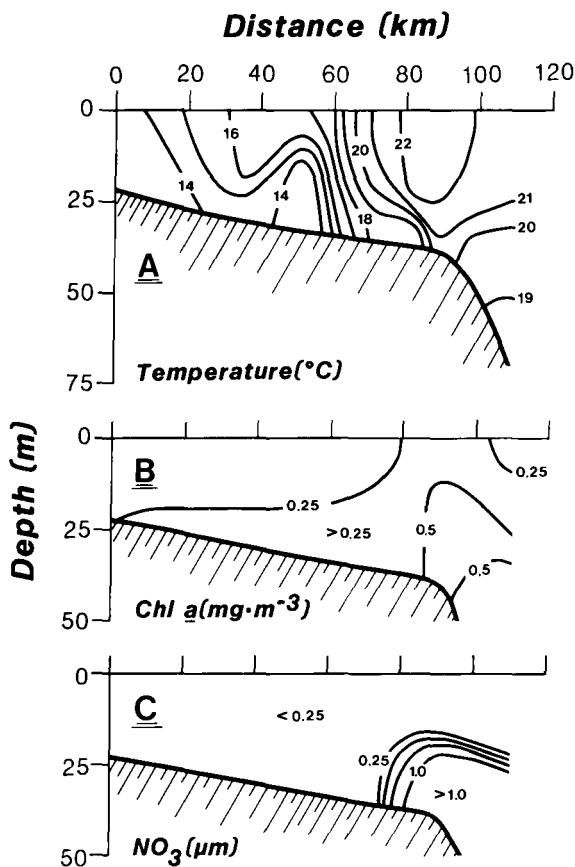
Seabird species feeding on fish displayed less affinity for the fronts because their prey are more mobile. The peak aggregation of piscivorous birds at the front (see Figure 5) may have been due to fish that were aggregated at the front for either zooplankton feeding or behavioral thermoregulation (Brandt and Wadley, 1981; Magnuson et al., 1981). Large schools of shoaling baitfish were observed at the front on 1 February 1984.

### *Influences of Front Heterogeneity*

Midshelf fronts are seasonally dynamic physical features. The formation of midshelf fronts typically begins in the northern South Atlantic Bight during fall as a result of atmospheric interactions with surface waters. Physical parameters of continental shelf waters off the Carolina coasts have been described by several authors (Bumpus, 1955; Bumpus, 1973; Stefansson et al., 1971). A marked wind shift from the southeast to the northwest occurs during fall in this region (Saunders, 1977; Weber and Blanton, 1980). Ekman forcing by northwest winds results in the retention of low-salinity, cooler-surface waters nearshore. Wind



**FIGURE 7.** Schematic cross-section relating a midshelf front to water masses and circulation on the southeastern United States continental shelf.



**FIGURE 8.** Cross-shelf section of a February 1982 midshelf front showing subsurface thermal structure (A) and concentrations of chlorophyll *a* (B) and nitrate (C).

events, namely the passage of cold fronts, concurrently cause intensified nearshore mixing and cooling (Brooks, 1978; Klinck et al., 1981), potentially abetted by intrusions of colder Virginia coastal waters (Bumpus and Pierce, 1955). As this nearshore zone of colder water forms, cross-shelf water surface temperature gradients are great enough to generate a second, midshelf zone between this water mass and the warmer outer shelf waters influenced by the Gulf Stream (Atkinson et al., 1983). Fron-

togenesis occurs as shelf waters form separate thermal zones (see Figure 7). As spring warming takes place, shelf waters become increasingly stratified as northerly wind events gradually decrease in duration and intensity. Fronts then break down (frontolysis) and decrease in spatial extent.

Seabird and front seasonality may be related because fronts are the principal mechanism enhancing foraging opportunities for this taxon within the midshelf domain. The secondary productivity associated with bottom intrusions is largely inaccessible to seabirds, except at fronts, since dominant species in this region are exclusively surface foragers (Haney, unpublished data).

Midshelf fronts are also subject to cross-shelf movements (see Figure 2). In late winter and spring, freshwater inputs to near-shore waters in the central portion of the South Atlantic Bight peak and allow a flux of low-salinity water offshore (Atkinson et al., 1978; Blanton and Atkinson, 1983). Generally, low-salinity water is removed by longshore currents adjacent to the coast. However, the increasing intermittency of strong, northerly wind events aided by low or southerly winds may advect lenses of low-salinity water offshore in plumes. When cross-shelf movement of water masses results from these events, the midshelf front becomes subject to Gulf Stream western boundary frontal dynamics, with both front types attaining nearly identical configurations (see Figures 1 and 3, *bottom*).

Cross-shelf movements of fronts may affect seabird distribution by shifting favorable foraging areas over a period of days. Seabird aggregations persist at fronts; large numbers of phalaropes were observed at the midshelf front on both 1 February and 8 February 1984, a period in which the front shifted 25 km seaward.

Seabirds may be affected by additional temporal and spatial heterogeneity exhibited by midshelf fronts. Alongshore seabird distribution within the midshelf domain may be influenced by the seasonal variation in the latitudinal occurrence of the fronts (see Figure 1). Significance of midshelf fronts to seabirds may depend not only on front number, length, and movement throughout the season of their occurrence, but also on variability over even

smaller spatial and shorter temporal scales. The intensity and duration of wind events, Gulf Stream frontal events, periodic tidal events, diurnal atmospheric change, and inherent frontal instability impart additional sources of variation to frontal dynamics (Garvine, 1974; Fearnhead, 1975; Bowman and Esaias, 1978; Brooks, 1978; Lee and Brooks, 1979; Allen et al., 1980; Brooks and Bane, 1981; Klinck et al., 1981). These effects may significantly influence conditions determining optimal seabird foraging at fronts (Briggs et al., 1984). Seabirds may forage efficiently at a given front at several different time intervals. The mobility of seabirds may allow them to make use of changes in favorable feeding opportunities when and wherever they occur.

### *Scale-Dependent Heterogeneity in Frontal Analyses*

The data presented here indicate that measurements of the temporal and spatial heterogeneity of fronts are important considerations when attempting to understand the coupling of physical and biological systems at these features, from both a biological and a sampling perspective (cf. Stommel, 1963; Kelley, 1976; Haury et al., 1978; Steele, 1978; Dayton and Tegner, 1984). Although fronts have been termed stable, predictable features with respect to seabird concentrations (Brown, 1980b), they may be highly variable oceanographic phenomena (Lee and Atkinson, 1983), and exert at least some corresponding variability on seabird distribution (Haney and McGillivray, 1985).

Scale of data analysis may affect conclusions regarding the associations between seabirds (or other marine organisms) and specific oceanographic features like fronts. Results from several tests presented here showed that reducing sample size and dropping degrees of freedom in the analyses altered the statistical results. In some cases this gave significant correlations when previous correlations were not significant. In other cases the probability of Type I error decreased, although not to the point of significance at the 5% level. Relating total seabird densities, and densities of particular species, to indices of midshelf fronts was thus meaningful only when information on frontal temporal and spatial boundaries was available beforehand and used to adjust the scale of analysis. These data were obtained by consulting

long series of satellite-derived charts gathered over several months.

The logistical problems involved in measuring the dynamic attributes of fronts are considerable (Bowman, 1978). One of the advantages of using remote sensing data for integrative work on marine ecosystems is that it allows real-time documentation of temporal and spatial patterns of physical oceanographic events at scales not normally possible with shipboard data collection. Examination of these trends may generate additional hypotheses relevant to biological systems. Ultimately, the testing of these hypotheses will allow a broader understanding of the ways in which marine organisms interact with their environment.

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